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Microclimate influence in a physiological model of cattle-fever tick (*Boophilus* spp.) population dynamics

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Abstract

Since their official eradication from the US in 1943, the cattle-tick species *Boophilus microplus* and *Boophilus annulatus*, vectors of bovine babesiosis, frequently have penetrated a quarantine zone established along the Texas–Mexico border designed to exclude them. Inspection and quarantine procedures have eradicated reinfestations successfully within the US, but increasing acaricide resistance in Mexican *B. microplus* populations poses a threat to future eradication efforts. Better understanding of interrelationships among *Boophilus* populations, their hosts, and vegetation communities in south Texas could improve prediction of the behavior of reintroduced *Boophilus* populations and increase management options. To this end, we constructed a simulation model to evaluate how microclimate, habitat (i.e. vegetation) heterogeneity, and within-pasture cattle movement may influence dynamics of *Boophilus* ticks in south Texas. Unlike previous *Boophilus* tick models, this model simulates dynamics at an hourly time-step, calculates all off-host dynamics as functions of temperature and relative humidity, and runs with ground-level microclimate data collected bi-hourly in three different habitat types. Sensitivity analysis of the model showed that temperatures and relative humidities created by habitat type, as well as engorged female mass, influenced tick population dynamics most strongly. Host habitat selection, initial number of larvae per cow, and the number of cells into which the simulated pasture was divided also had a strong influence. Population dynamics appeared moderately sensitive to the proportion of *Bos indicus* in cattle genotypes and the larval attachment rate, while appearing relatively insensitive to factors such as mortality rate of engorged females. When used to simulate laboratory experiments from the literature, the model predicted most observed life-history characteristics fairly well; however, it tended to underestimate oviposition duration, incubation duration, and egg mortality and overestimate larval longevity, especially at low temperatures and high humidities. Use of the model to predict *Boophilus* population dynamics in hypothetical south Texas pastures showed that it reasonably generated qualitative patterns of stage-wise abundances but tended to overestimate on-host tick burdens. Collection and incorporation of data that appear not to exist for *Boophilus* ticks, such as larval lipid content and lipid-use rates, may improve model accuracy. Though this model needs refinements such as a smaller spatial resolution, it provides insight into responses of *B. microplus* or *B. annulatus* populations to specific weather patterns, habitat heterogeneity, and host movement.

Keywords: Simulation model; *Boophilus annulatus*; *Boophilus microplus*; Microclimate; Physiological age; Host movement; Texas

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1. Introduction

Though eradicated from the US, the cattle-tick species *Boophilus microplus* and *Boophilus annulatus*, vectors of bovine babesiosis, continue to cause considerable concern in the US because both species remain just across the US–Mexico border. To date, inspection and quarantine methods have eradicated all detected outbreaks in the US successfully, but development of insecticide resistance in Mexican *B. microplus* ticks challenges the integrity of the US eradication program (George et al., 2002). Systems analysis and simulation already have been used to analyze interactions among *Boophilus* ticks, cattle, and landscape in south Texas (Weidhaas et al., 1983; Mount et al., 1991; Teel et al., 1996, 1997, 1998, 2003; Corson et al., 2001, 2003); however, the structural or temporal resolutions of these models reduce their ability to capture the crucial influence of microclimate on arthropod physiology and phenology, both of which drive population dynamics (Miller et al., 1973). A model built at a smaller temporal scale and containing more detailed representation of the relationships between microclimate and life-history characteristics may provide greater insight into system processes and improve prediction of system behavior. We attempted to do so by explicitly simulating the effects of microclimate temperature and saturation deficit on *Boophilus* ticks. Saturation deficit, a function of temperature and relative humidity (RH), indicates the dryness of the air and greatly influences survival of *Boophilus* eggs and larvae (Edney, 1982; Teel, 1984). In this study, we focused on modeling the influence of microclimate conditions, as driven by habitat type (i.e. vegetation), on tick–cattle–landscape interactions in the biotic region of south Texas, the Tamaulipan biome. We approached this problem with the understanding that *B. microplus* and *B. annulatus* represent tropical and temperate species, respectively, and overlap in distribution in this biome (Graham and Hourrigan, 1977). Differences in temperature-specific life-history characteristics appeared slight enough for the purposes of this model to use data from both species for model development and evaluation.

2. Model description

Boophilus ticks, their cattle hosts, and vegetation-mediated microclimate in a south Texas pasture serve as this model's system of interest. The deterministic compartment model was developed using the software package STELLA 6.0 (High Performance Systems Inc., Hanover, NH, USA) on a personal computer. The model simulates dynamics with difference equations and uses an hourly time-step for all life stages, the first model of the complete *Boophilus* spp. life cycle known to do so. To provide greater flexibility and generality, temperature and saturation deficit, rather than time, drive nearly all off-host development, fecundity, mortality, and activity rates in the model; thus, the model simulates implicit physiological age, rather than chronological age, of off-host ticks (Uspensky, 1995). Conceptually, the model contains submodels representing (1) environmental conditions, (2) off-host tick life-history characteristics, (3) on-host tick life-history characteristics, and (4) vegetation composition (grass versus woody species) in a 100 ha pasture (Fig. 1). Table 1 lists model input and output variables and parameter values.

2.1. Environmental submodel

This submodel contains historical microclimate temperature and RH experienced by ticks at ground level in different habitat types. The model was developed with environmental data from a laboratory study of *B. annulatus* survival and development (Teel et al., unpublished) that approximated the temperatures and RHs observed by Fleetwood (1985) from 1981 to 1982 in mid-successional pastures near La Gloria, Texas (27.3°N, 98.1°W). Fleetwood (1985) collected bi-hourly data at ground level in each of three habitat types: uncanopied buffelgrass (*Cenchrus ciliaris*), mixed-brush-canopied buffelgrass, or mesquite (*Prosopis glandulosa*)-canopied buffelgrass (hereafter called "grass", "mixed brush", and "mesquite", respectively). The model linearly interpolates between data points to estimate temperature and RH at hours not provided by the data; it calculates saturation deficit according to Rosenberg et al. (1983).

2.2. Engorged female preoviposition and oviposition submodel

This submodel tracks engorged females that detach from cattle and estimates durations of their preoviposition periods, their mortality rates, and the rate at which

Table 1
Values of input and output variables and parameters used in the model

Variable or constant	Initial value
Tick abundance state variables[a]	
Engorged females that detached on day *X*, preoviposition period	0
Engorged females that detached on day *X*, oviposition period	0
Eggs laid on day *X*	0
Off-host larvae that hatched on day *X*, hardening period	0
Off-host larvae that hatched on day *X*, questing period	0
On-host larvae 0 days old on average cow	50
On-host larvae >0 days old on average cow	0
Nymphs *X* days old on average cow	0
Adult males *X* days old on average cow	0
Adult females *X* days old on average cow, engorging	0
Adult females *X* days old on average cow, engorged (>4.5 mm)	0
Physiology state variables[a]	
Proportion of preoviposition completed for engorged females that detached on day *X*	0
Cumulative saturation-deficit hours >4 mmHg for engorged females that detached on day *X*	0
Cumulative degree-hours >16 °C for engorged females that detached on day *X*	0
Cumulative degree-hours <16 °C for engorged females that detached on day *X*	0
Cumulative proportion of total eggs laid by females that detached on day *X*	0
Proportion of development completed by incubating eggs laid on day *X*	0
Cumulative saturation-deficit hours >0 mmHg for eggs laid on day *X*	0
Cumulative degree-hours <16 °C for eggs laid on day *X*	0
Cumulative saturation-deficit hours >4 mmHg for off-host larvae that hatched on day *X*	0
Cumulative degree-hours >16 °C for off-host larvae that hatched on day *X*	0
Chronological age of off-host larvae that hatched on day *X*	0
Cumulative tick exposure-hours of average cow	0
Parameters	
Initial day of year	1
Number of cows in herd	80
Size of pasture (ha)	100
Upper lethal temperature for all off-host stages (1 h exposure) (°C)	60
Lower lethal temperature for eggs (1 h exposure) (°C)	−13
Lower lethal temperature for off-host larvae (1 h exposure) (°C)	−5
Threshold for cumulative saturation-deficit hours for off-host engorged females and larvae (mmHg)	4
Threshold for cumulative saturation-deficit hours for eggs (mmHg)	0
Threshold for cumulative degree-hours for off-host engorged females and larvae (°C)	16
Cumulative saturation-deficit hours causing death of off-host engorged females (mmHg h)	20000
Cumulative saturation-deficit hours causing death of eggs (mmHg h)	15623
Minimum cumulative saturation-deficit hours causing death of off-host larvae (mmHg h)	324
Maximum cumulative saturation-deficit hours causing death of off-host larvae (mmHg h)	5557
Cumulative degree-hours <16 °C that begin to decrease female CEI (°C h)	4500
Cumulative degree-hours <16 °C that begin to increase egg mortality (°C h)	360
Cumulative degree-hours causing death of off-host engorged females (°C h)	16872
Maximum cumulative degree-hours causing death of off-host larvae (°C h)	17766
Maximum chronological age of off-host larvae (days)	253
Hourly predation rate of off-host engorged females	0.063
Hourly development rate of eggs at 25 °C	0.0020417
Temperature at which rate-controlling enzyme becomes half active and half high-temperature inactive	307.7 K (34.7 °C)
Temperature at which rate-controlling enzyme becomes half active and half low-temperature inactive	284.7 K (11.7 °C)
Change in heat content associated with high-temperature inactivation of the enzyme	85023.39
Change in heat content associated with low-temperature inactivation of the enzyme	−55787.19
Heat content of activation associated with the reaction catalyzed by a rate-controlling enzyme	21525.72
Universal gas constant	1.987

Table 1 (*Continued*)

Variable or constant	Initial value
Density of questing larvae at which cattle detect and avoid all larvae (i.e. no pick-up) (million/ha)	10
Mass of each engorged female (mg)	300
Number of eggs per mg of egg mass	20
Time spent on host by larvae (days)	≤6
Time spent on host by nymphs (days)	7–14
Time spent on host by adult males (days)	≥15
Time spent on host by undetectable adult females (days)	15–18
Time spent on host by detectable adult females, which begin to detach (days)	≥19
Maximum time a cohort (males and females) remains on host (days)	35
Male:female sex ratio on host	1:1.36
Hourly decrease in amount of tick exposure (accumulated "tick-hours")	0.00274
Number of on-host detectable ticks causing host mortality due to acute tick exposure	3000
Number of on-host detectable ticks causing host mortality due to chronic tick exposure after 90 days	1000

[a] State variables are arrayed by up to three cells within the pasture.

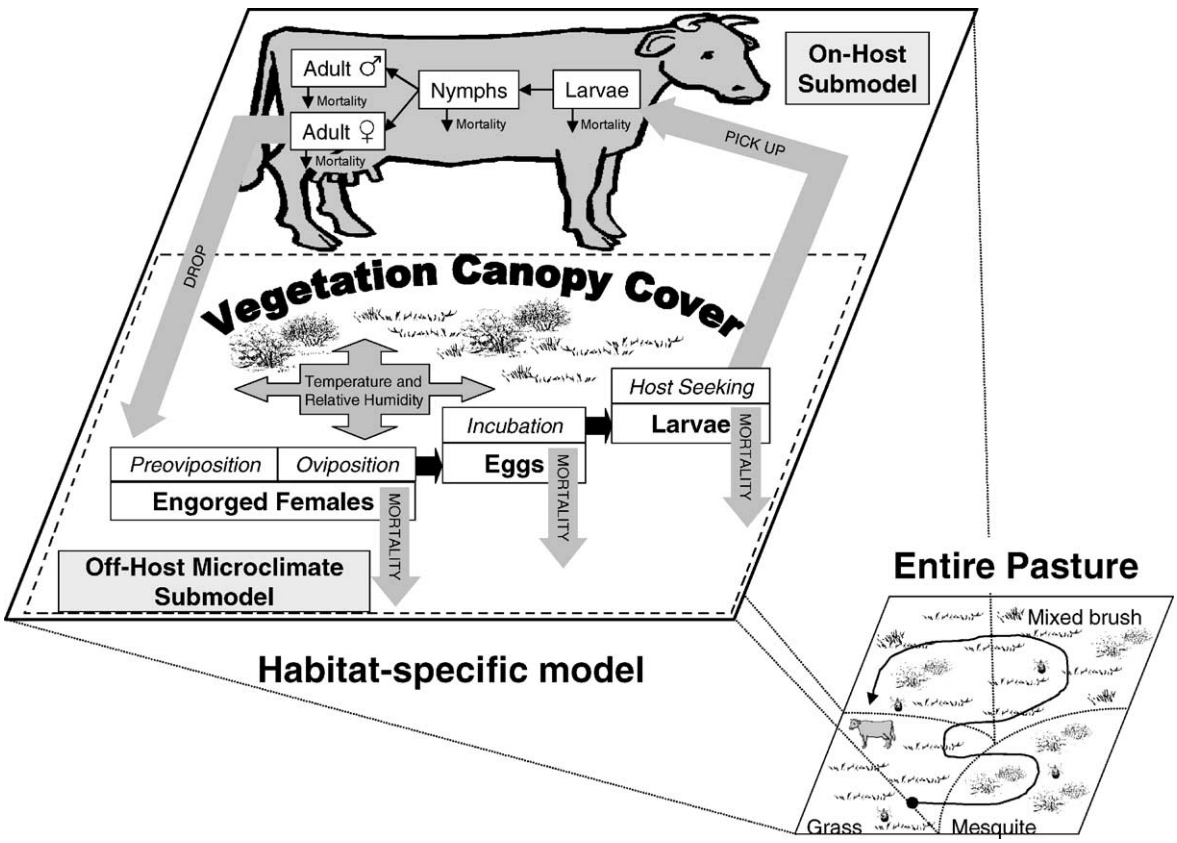

Fig. 1. Conceptual diagram of the tick–cattle–landscape model.

they lay eggs. All females detaching on the same day enter that day's cohort, whose members each will experience the same development, oviposition, and mortality rates.

2.2.1. Duration of engorged female preoviposition period

To estimate duration of preoviposition in response to fluctuating temperatures, data from Jagannath et al. (1982), Ouhelli et al. (1982), and Davey (1988) for length of preoviposition period (in days) for *B. annulatus* at several constant temperatures were merged and transformed to hourly "rates of completion". A reciprocal quadratic curve was fitted to these transformed data ($n = 12$, $R^2 = 0.912$) so that hourly rate of completing preoviposition changes with temperature:

$$\text{PO\_RATE} = \frac{1}{631.45 - 35.75T + 0.546T^2} \quad (1)$$

where T is the microclimate temperature (°C).

With this equation, preoviposition duration decreases to a minimum of 2 days around 33 °C. The lower boundary of this curve's range is set at 12 °C, following observation that engorged *B. annulatus* females failed to oviposit at or below this constant temperature (Davey, 1988).

2.2.2. Engorged female mortality

To reflect female mortality due to desiccation, the model monitors each cohort's cumulative saturation-deficit hours (CSDH), calculated as the cumulative sum of saturation deficit minus 4 mmHg each hour, a body-water recuperation threshold for post-embryonic stages of ixodid ticks (Teel et al., unpublished). Saturation deficits below 4 mmHg add nothing to CSDH. A cohort of engorged females in the model dies if it accumulates ≥20,000 mmHg h (saturation-deficit hours), a conjectured threshold set arbitrarily higher than those for eggs and larvae to reflect the greater resistance of engorged females to desiccation (Hitchcock, 1955a). To represent influence on female mortality of temperature alone, a degree-day model developed by de la Vega and Díaz (1987) was adapted. Their model accumulated the degrees >16 °C experienced by off-host *B. microplus* larvae and considered that the last larva in a cohort died when this sum equaled 703 °C-days. Applied to engorged females, this threshold is converted to hourly units in our model so that death of an engorged female cohort occurs at 16,872 °C h (cumulative degree-hours, CDH). Preliminary simulations revealed that using this model alone fails to capture female mortality at temperatures ≥40 °C; so, a line was fitted to time–temperature mortality data for *B. microplus* (Hitchcock, 1955a; Bennett, 1974) that increases accumulating degree-hours for off-host engorged females (FEM_CDH) as temperatures increase ≥40 °C ($n = 5$, $R^2 = 0.995$):

$$\begin{aligned} &\text{FEM\_CDH} = (T - 16)(-396.2426 + 10.0482T), && T \geq 40\,^\circ\text{C} \\ &\text{FEM\_CDH} = (T - 16), && T < 40\,^\circ\text{C} \end{aligned} \quad (2)$$

where T is the microclimate temperature (°C).

Given the upper lethal temperatures reported by Hitchcock (1955a) for *B. microplus*, 1 h exposure to 60 °C is set as the upper lethal temperature for this and all other tick stages. To reflect mortality due to predation, cohorts of engorged females in the model suffer 10% mortality per week (0.063% per hour) (Sutherst et al., 2000). Females begin laying eggs upon completion of the preoviposition period.

2.2.3. Engorged female fecundity

Next, a quadratic curve was fitted to data from Davey (1988) and Bennett (1974) showing mean conversion efficiency index (CEI) (i.e. proportion of body weight converted to egg weight) of *B. annulatus* and *B. microplus*, respectively, at constant temperatures ($n = 17$, $R^2 = 0.899$):

$$\text{CEI} = -159.08 + 16.63T - 0.3136T^2 \quad (3)$$

where T is the microclimate temperature (°C).

Using this equation, CEI reaches a maximum of 0.615 at 26.5 °C. Some researchers noted that CEI decreases with constant exposure to cold (Bennett, 1974; Davey, 1988); consequently, data from Bennett (1974) were used to decrease CEI as a function of accumulated hourly temperatures *below* a threshold of 16 °C, but only when cumulative cold degree-hours for off-host females exceed 4500 °C h:

$$\begin{aligned} &\text{CEI} = \text{CEI}, && \text{CCDH} \leq 4500 \\ &\text{CEI} = \text{CEI} - 0.004 \times \text{FEM\_CCDH}, && \text{CCDH} > 4500 \end{aligned} \quad (4)$$

where CEI is the previously calculated hourly conversion efficiency index, FEM_CCDH the cumulative

degree-hours below 16 °C for a cohort of engorged females.

The model then uses CEI to calculate the maximum number of eggs a female can lay at a given temperature:

$$\text{MAX\_EGGS} = \text{MASS} \times \text{CEI} \times 20 \quad (5)$$

where MASS is the mass of one ovipositing female (mg).

Mass of individual engorged females is set at a constant 300 mg, the approximate midpoint of reported *B. microplus* weight extremes (Davey et al., 1980b; Ouhelli et al., 1982). The number *Boophilus* eggs in each mg of eggs laid is set at 20 (de la Vega, 1976).

2.2.4. Engorged female egg production

To estimate the temperature-dependent rate at which females lay eggs, data were obtained from laboratory studies of *Boophilus* egg production at constant temperatures (Bennett, 1974; Davey, 1981, 1986, 1988). From these studies, oviposition data at 13 temperatures from 12.8 to 45.0 °C were selected and converted to daily cumulative proportion of total eggs laid at each temperature. Then, the previous day's cumulative proportion was subtracted from that for the current day and divided by 24 to obtain an hourly rate of oviposition during each day of oviposition at each temperature. Using cumulative proportion of total eggs laid as the independent variable and its hourly rate as the dependent variable, a polynomial curve was fitted to each temperature's data (Table 2). With this method, at each temperature, the proportion of total eggs a female already has laid determines the hourly rate at which she continues to lay them. By multiplying the hourly oviposition rate by MAX_EGGS, the model estimates number of eggs laid per female each hour. Each temperature's curve covers a 1.6–3.6 °C range of temperatures around it, and as temperatures change beyond this range, the model changes the curve used. Below 14.2 °C and above 41.9 °C females lay no eggs; egg production peaks at 33.6–36.4 °C. Thus, temperature variations change both the potential number of eggs a female can produce and the rate at which she can produce them. To avoid abnormally long oviposition periods as cumulative oviposition moves asymptotically toward the maximum, a cohort of females dies when it has laid 97% of its potential eggs. As with off-host females before oviposition, a cohort of ovipositing females dies if temperature ≥60 °C, CSDH ≥20,000 mmHg h, or CDH ≥16,782 °C h.

Table 2
Equations and data sources used in the model to estimate at different temperatures hourly proportion of total eggs laid (y) as a function of cumulative proportion of total eggs already laid (x)

Observed temperature (°C)	Covers temperature range (°C)	Equation	Statistics and source
12.8	<14.17	$y = 0$	$n = 1$[a]
15.6	≥14.17 to <16.95	$y = 0.00007 + 0.015x - 0.043x^2 + 0.044x^3 - 0.016x^4$	$n = 70$, $R^2 = 0.697$[a]
18.3	≥16.95 to <19.72	$y = 0.00013 + 0.022x - 0.063x^2 + 0.068x^3 - 0.028x^4$	$n = 42$, $R^2 = 0.861$[a]
21.1	≥19.72 to <22.50	$y = 0.00053 + 0.034x - 0.102x^2 + 0.115x^3 - 0.047x^4$	$n = 30$, $R^2 = 0.891$[a]
23.9	≥22.50 to <24.45	$y = 0.00082 + 0.040x - 0.113x^2 + 0.118x^3 - 0.046x^4$	$n = 22$, $R^2 = 0.802$[a]
25.0	≥24.45 to <26.00	$y = 0.00341 + 0.013x - 0.012x^2 - 0.020x^3 + 0.016x^4$	$n = 20$, $R^2 = 0.974$[b]
27.0	≥26.00 to <28.22	$y = 0.00460 + 0.012x - 0.030x^2 + 0.023x^3 - 0.010x^4$	$n = 19$, $R^2 = 0.999$[c]
29.4	≥28.22 to <30.83	$y = 0.00124 + 0.072x - 0.212x^2 + 0.226x^3 - 0.088x^4$	$n = 15$, $R^2 = 0.942$[a]
32.2	≥30.83 to <33.61	$y = 0.00117 + 0.073x - 0.196x^2 + 0.187x^3 - 0.065x^4$	$n = 14$, $R^2 = 0.949$[a]
35.0	≥33.61 to <36.39	$y = 0.00248 + 0.065x - 0.148x^2 + 0.107x^3 - 0.027x^4$	$n = 12$, $R^2 = 0.999$[a]
37.8	≥36.39 to <38.34	$y = 0.00234 + 0.064x - 0.184x^2 + 0.187x^3 - 0.070x^4$	$n = 13$, $R^2 = 0.988$[a]
38.9	≥38.34 to <41.95	$y = 0.00042 + 0.069x - 0.165x^2 + 0.141x^3 - 0.044x^4$	$n = 14$, $R^2 = 0.946$[a]
45.0	≥41.95	$y = 0$	$n = 1$[d]

[a] *B. microplus* (Bennett, 1974).
[b] *B. annulatus* (Davey, 1986).
[c] *B. microplus* (Davey, 1981).
[d] *B. annulatus* (Davey, 1988).

2.3. Egg submodel

This submodel estimates durations of egg incubation periods (a function of egg development rates), egg mortality rates, and durations of egg hatching. All eggs laid on the same day enter the same daily cohort, whose members each will experience the same development, mortality, and hatch rates.

2.3.1. Egg development rate

To estimate the time until first hatch of an egg cohort, a function of development rate, the rate-summation embryonic development model for *B. annulatus* from Strey et al. (1991) was included:

$$\text{EGG\_DEV\_RATE} = \frac{\text{RHO25}(T/298.15)\, e^{[(\text{HA}/r)((1/298.15)-(1/T))]}}{1 + e^{[(\text{HL}/r)((1/\text{TL})-(1/T))]} + e^{[(\text{HH}/r)((1/\text{TH})-(1/T))]}} \quad (6)$$

where RHO25 represents the hourly development rate at 25 °C, TH the temperature (K) at which rate-controlling enzyme becomes half active and half high-temperature inactive, TL the temperature (K) at which rate-controlling enzyme becomes half active and half low-temperature inactive, HH the change in heat content associated with high-temperature inactivation of the enzyme, HL the change in heat content associated with low-temperature inactivation of the enzyme, HA the heat content of activation associated with the reaction catalyzed by a rate-controlling enzyme, r the universal gas constant, T the ground temperature (K).

Strey et al. (1991) reported that model estimates of time to first hatch fit observed emergence dates well ($R^2 = 0.9964$, $P < 0.0001$).

2.3.2. Egg mortality rate

Because *Boophilus* eggs cannot exchange water actively, their mortality rate depends heavily on saturation deficit (Teel, 1984). The laboratory data of *B. annulatus* from Teel et al. (unpublished) were used to estimate mortality of an entire egg cohort as a function of CSDH at first hatch ($n = 508$, $R^2 = 0.402$):

$$\text{EGG\_MORT\_PROP} = 0.169 + 0.000086x - 2.1 \times 10^{-9}x^2 \quad (7)$$

where x is the CSDH (mmHg h) of egg cohort at first hatch.

Unlike for female and larval CSDH, the model does not subtract a minimum threshold of 4 mmHg from hourly saturation deficit for eggs, which reflects the inability of eggs to recoup lost water. Based on *B. microplus* data from Gothe (1967), lower lethal temperature for eggs is set at −13 °C (1 h exposure). Research shows that egg mortality increases with exposure to cold temperatures (Bennett, 1974; Davey, 1988). To represent the additive egg mortality caused by cold temperatures, *B. annulatus* data from Davey (1988) were used to increase egg cohort mortality as a function of accumulated hourly temperatures *below* a threshold of 16 °C, but only when cumulative cold degree-hours for eggs exceeded 360 °C h:

$$\begin{aligned} &\text{EGG\_MORT\_PROP} \\ &\quad = \text{EGG\_MORT\_PROP}, && \text{CCDH} \le 360 \\ &\text{EGG\_MORT\_PROP} && \\ &\quad = \text{EGG\_MORT\_PROP} && \\ &\qquad + 0.0001 \times \text{EGG\_CCDH}, && \text{CCDH} > 360 \end{aligned} \quad (8)$$

where EGG_MORT_PROP is the previously calculated cumulative mortality rate of egg cohort, EGG_CCDH the cumulative degree-hours below a threshold of 16 °C for an egg cohort.

Egg cohorts that complete development before the mortality proportion equals 1 begin to hatch, at which time the model applies the current mortality proportion to the cohort.

2.3.3. Duration of egg hatch

Data from Strey et al. (1991) showed that mean duration of egg hatch at different temperatures equaled ≈77% of the time required to achieve first hatch. For surviving eggs in each cohort, the model approximates temporal distribution of egg hatch with a Weibull distribution ($n = 21$, $R^2 = 0.997$):

$$\text{CUM\_PROP\_HATCHED} = 1.005 - 0.98\, e^{-0.014x^{10.424}} \quad (9)$$

where x is the normalized development time (multiples of time to first hatch).

At first hatch, a cohort's normalized development time equals 1. The proportion of eggs hatching

changes as hatch proceeds, and mean (50%) hatch occurs at a normalized development time of 1.46. Egg hatch continues until remaining eggs in the cohort hatch at a normalized development time of 1.77 or die, which occurs when temperature ≤ -13 or $\geq 60\,^{\circ}C$ or incubation CSDH $\geq 15{,}623$ mmHg h.

2.4. Larval submodel

This submodel estimates larval longevities (a function of larval mortality rates) and host-finding rates. Larvae emerging from eggs on the same day enter the same daily cohort, whose members each will experience the same mortality, development, and activity rates.

2.4.1. Larval mortality rate

Based on *B. microplus* data from Gothe (1967), lower lethal temperature for larvae is set at $-5\,^{\circ}C$ (1 h exposure). The mean CSDH of the first egg cohorts hatching into a daily larval cohort determines the threshold CSDH at which larvae in that cohort die. This mechanism reflects the influence of stress received as an embryo on larval longevity (i.e. appearance of the first larva to the death of the last larva in an egg mass); as egg stress increases, larval longevity decreases (Maywald, 1987). To estimate this threshold, a line was fitted to data from Teel et al. (unpublished) for *B. annulatus* larval CSDH at death as a function of CSDH accumulated as an egg ($n = 1250$, $R^2 = 0.339$):

$$\text{LARV\_CSDH\_LIMIT} = 5557.3 - 0.335x \tag{10}$$

where x is the CSDH (mmHg h) accumulated as an egg.

To represent the time required for exoskeletons of newly hatched larvae to harden, the model forces larval cohorts to wait 96 h before they can attach to hosts within the same habitat cell (Davey, 1987). Once capable of attaching to hosts, each larval cohort suffers an hourly mortality rate equal to the inverse of the difference between its CSDH mortality threshold (LARV_CSDH_LIMIT) and its current CSDH value. Given their ability to retain and recoup water, larvae, like engorged females, accumulate hourly only the amount of saturation deficit greater than 4 mmHg. Using only this method to estimate mortality rate, however, would overestimate larval longevity under conditions of high humidity, when larvae experience little or no water-balance stress. To represent influence on larval mortality of temperature alone, a line was fitted to data from Teel et al. (unpublished) for *B. annulatus* larval CDH at death as a function of CSDH accumulated as an egg ($n = 464$, $R^2 = 0.195$):

$$\text{LARV\_CDH\_LIMIT} = 17765.9 - 0.812x \tag{11}$$

where x is the CSDH (mmHg h) accumulated as an egg.

Therefore, with these two measures of larval mortality working together, hourly mortality rate is a function of temperature and CSDH, equaling 1 only if temperature ≤ -5 or $\geq 60\,^{\circ}C$, CSDH $\geq$ LARV_CSDH_LIMIT, or CDH $\geq$ LARV_CDH_LIMIT. Simulated larvae remain in the pasture until they die or attach to a host. To ensure that larval longevities calculated from these physiological equations do not exceed observed chronological longevities, the model limits larval longevity to 253 days, the longest reported mean survival of *Boophilus* larvae observed under field temperatures (Cotton, 1915).

2.4.2. Larval host-finding rate

To estimate the host-finding rate, the proportion of larvae encountered and picked up hourly by the cattle herd, equations were adapted from the BCTSIM model of Mount et al. (1991) that calculated host-finding rate (HFR) as a function of a base host-finding rate (BHFR), a temperature-effect multiplier (TE), and a larval-density effect multiplier (LDE):

$$\text{HFR} = \text{BHFR} \times \text{TE} \times \text{LDE} \tag{12}$$

The base hourly host-finding rate increases as cattle density (D, cows/ha) increases, according to the following formula:

$$\text{BHFR} = \frac{(0.203777 \times D^{0.514573})}{168} \tag{13}$$

The multipliers used to modify this value, TE and LDE, have values bounded between 0 and 1. TE represents the increase in larval-questing activity prompted by an increase in temperature. Of two TE equations in Mount et al. (1991), we selected that for *B. microplus*, which peaks $\approx 4\,^{\circ}C$ higher than that for *B. annulatus*:

$$\text{TE} = -4 + 0.4T - 0.008T^2 \tag{14}$$

where T is the microclimate temperature (°C).

LDE represents the ability of cattle to detect and avoid dense patches of questing larvae; as densities of questing larvae increase, LDE decreases, reducing the host-finding rate:

$$\text{LDE} = -0.5 \times \log_{10}(\text{LARVAL\_DENSITY}) + 3.5 \quad (15)$$

where LARVAL_DENSITY is the number of questing larvae per ha.

Given this equation, cattle detect and no longer pick up larvae if questing larval density exceeds 10 million/ha. The model calculates larval density as a function of the area of the habitat cell in which the larvae live. Likewise, as the cattle herd in the model roam among up to three cells, its density changes with the area of the habitat cell it visits. The model calculates number of larvae picked up by the herd each hour as the number of questing larvae in a habitat times the host-finding rate. The model divides total pick-up by the number of questing larval cohorts to find the mean number of larvae picked up per cohort, which the model subtracts from each cohort. It then divides the total pick-up equally among all cattle in the herd to determine how many larvae attach to the single "average" cow simulated in the model. Although field studies have shown that individual cows in the upper and lower tiers of herd hierarchy carry higher tick burdens than individuals in the middle tier (Aguilar and Solis, 1984), dividing picked-up larvae evenly among all cattle in the herd seems reasonable given the coarse spatial scale of the model.

2.5. On-host tick submodel

This submodel estimates the on-host tick development, mortality, and detachment rates. All larvae attaching on the same day enter the same daily cohort, whose members each will experience the same development and mortality rates.

2.5.1. On-host tick development rate

Because environmental temperature surrounding the host has little influence on the duration of the parasitic phase (Hitchcock, 1955b), on-host biological processes are controlled with time rather than temperature. The model represents five subgroups of on-host *Boophilus* ticks, defined by the amount of time they have spent on the host: (1) larvae (≤6 days), (2) nymphs (7–14 days), (3) adult males (≥15 days), (4) undetectable adult females (15–18 days), and (5) detectable adult females (≥19 days). Durations of life stages were set using *B. microplus* data (Hitchcock, 1955b; Roberts, 1968).

2.5.2. On-host tick mortality rate

During each stage of development, on-host cohorts experience an hourly mortality rate adapted from Mount et al. (1991) for *B. microplus* on either *Bos taurus* or *Bos indicus* hosts (Table 3). This mortality rate varies with innate host resistance (*Bos indicus* ≫ *Bos taurus*) and amount of on-host tick exposure (accumulated "tick-hours"), representing gain and loss of host resistance. Above and below the thresholds indicated, the model applies the mortality rate listed for the nearest threshold; between thresholds, it linearly interpolates to find mortality rate. The hourly decrease in amount of tick exposure equals 0.00274. Ticks that survive 14 days on-host molt into adult males and females, using a male:female sex ratio of 1:1.36 (Davey and Cooksey, 1988).

Table 3
Hourly mortality rates of parasitic larvae, nymphs, and adult *B. microplus* on *Bos taurus* or *Bos indicus* cattle as a function of lower and upper "tick-hour" thresholds on the average cow (converted from Mount et al., 1991)

Stage (days on host)	Lower and upper "tick-hour" thresholds			
	168,000 tick-hours		2,520,000 tick-hours	
	B. taurus	*B. indicus*	*B. taurus*	*B. indicus*
Larvae (0–6 days)	0.0059	0.0073	0.0098	0.0121
Nymphs (7–14 days)	0.0002	0.0008	0.0031	0.0053
Adults (≥15 days)	0.0014	0.0020	0.0045	0.0069

Below the lower and above the upper thresholds, the model applies the mortality rate listed for the nearest threshold; between thresholds, it linearly interpolates to find mortality rate.

2.5.3. On-host tick detachment rate

Adult females reach a detectable size (>4.5 mm) 19 days after attachment and begin to detach from the host at an hourly rate obtained by fitting a quadratic curve through *B. microplus* data from Hitchcock (1955b) ($n = 16$, $R^2 = 0.647$):

$$\text{DETACH\_RATE} = -0.123 + 0.010x - 0.00018x^2 \quad (16)$$

where x is the day of on-host development (limited to days 19–35).

Adult males remain on the host until 36 days after attachment, when the model removes any ticks remaining in the cohort.

2.6. Host mortality

The model allows mortality of hosts to occur due to acute or chronic blood loss caused by high tick burdens on the average cow. In field experiments, cattle that carried 200–465 detectable engorged females per day for 8 months either died or required removal from experiments (Bourne et al., 1988). The largest reported number of detectable engorged females counted on a cow was 1366 on one side of a *Bos taurus* individual (Wharton et al., 1969). Based on these values, mortality due to acute tick exposure occurs in the model if the detectable tick burden on the average cow exceeds 3000. Mortality due to chronic exposure occurs if the detectable tick burden exceeds 1000 on more than 2160 non-consecutive hours (90 days); the count increases by 1 each hour that detectable tick burden >1000 and decreases by 1 (down to zero) each hour that detectable tick burden $\leq$1000. The model simulates host mortality by decreasing the number of on-host ticks of all stages by 95% on the average cow, emulating mortality of cows in the herd with the highest tick burdens. The remaining on-host ticks represent those on surviving cows, which would have lower tick burdens (and usually higher innate host resistance) than the average cow simulated. Though not as ideal as simulating the individual tick burden of each cow in the herd, this mechanism provides negative feedback to tick population growth, which otherwise would produce vast overestimates of on-host tick burdens.

2.7. Spatial resolution and host movement

The model simulates 80 cows inhabiting a 100 ha pasture divided into 1–3 habitat cells, each of which represents a grass, mixed-brush, or mesquite habitat. The hourly time-step of the model allows specification of a daily time-budget for cattle, with potential movement each hour based on habitat-preference probabilities. Before using the model to predict *Boophilus*-population dynamics in hypothetical scenarios, we first evaluated how sensitive model output appeared to changes in key factors and how well it simulated observed data.

3. Model evaluation

3.1. Sensitivity analysis

Model sensitivity to several parameters was examined under simulated field conditions. Number of questing larvae was selected as the output of interest since it plays an important role in longevity and dispersal of *Boophilus* infestations. The baseline simulation consisted of a 2-year simulation of a *Boophilus* infestation started with 50 newly attached larvae per cow introduced on 25 March (spring) by a herd of 80 *Bos taurus* cattle in a 100 ha mesquite-canopied pasture. Because the model ran relatively slowly (30–90 min per simulated year) model evaluation runs simulated only 2 years each. The first year of temperature and RH data from the previously described incubator study (Teel et al., unpublished) was used to represent weather in each simulated year (i.e. year 1 data repeated for year 2). For each change in an input parameter, the corresponding change in peak number of questing larvae was recorded for each year of the 2-year simulations. Parameters were varied individually and a normalized sensitivity index (S) was calculated using the following equation:

$$S = \frac{(O_H - O_L)/O_M}{(I_H - I_L)/I_M} \quad (17)$$

where I_H is the higher value of the input parameter, I_L the lower value of the input parameter, I_M the mean of the two input values, O_H the corresponding output for the higher input value, O_L the corresponding output

Table 4
Sensitivity analysis index (S) of number of questing larvae in year 1 and 2 of 2-year simulations for the specified variations in species-specific model parameters, sorted from highest to lowest mean of the absolute values of S (see text for explanation of S)

Parameter	Variation (%)	Year 1	Year 2	Mean $\|S\|$
Microclimate temperature	±25	3.68	3.58	3.63
Engorged female mass	±25	1.81	1.57	1.69
Microclimate relative humidity	±25	2.24	0.71	1.47
Number of cells into which pasture is divided	±50	−1.28	−1.28	1.28
Initial larvae per cow	±20	0.38	−1.91	1.14
Proportion of day spent in grass half of a 50% grass/50% mesquite pasture	±50	−1.55	−0.58	1.06
Threshold CSDH causing larval death	±20	0.30	1.43	0.87
Proportion of *Bos indicus* in cattle genotypes	±100	−0.61	−0.59	0.60
Larval attachment rate	±25	0.91	0.14	0.53
Incubation temperature at which rate-controlling enzyme is half active and half low-temperature inactive (in °C)	±116	−0.70	−0.18	0.44
Time each day cattle start a half-day stay in the mesquite half of a 50% grass/50% mesquite pasture	±50	−0.24	−0.31	0.28
Engorged female mortality rate	±100	−0.14	−0.33	0.23
Proportion of grass area in grass/mesquite pasture (time spent in each habitat equal)	±50	0.11	0.25	0.18
Time for larval hardening	±25	0.13	0.06	0.09
Threshold CSDH causing engorged female death	±85	0.00	0.00	0.00

for the lower input value, O_M the mean of the two output values.

For example, an S index of 1.0 means that output changed in a direct and equal proportion over the range of change in input (e.g. ±10% = 20%), while an S index of −0.5 means that output changed only 50% as much in an inverse direction to the change in input.

Sensitivity analysis results (Table 4) indicated that peak size of questing larvae populations appeared most sensitive to microclimate temperature (mean $|S| = 3.63$); in the relatively moderate temperatures found under mesquite canopies, increasing temperature greatly increased number of questing larvae. Predicted peak number of questing larvae appeared next most sensitive to engorged female mass (mean $|S| = 1.69$), which directly increased fecundity as female mass increased. Microclimate RH had the next strongest influence (mean $|S| = 1.47$), increasing peak number of questing larvae as it increased. The number of cells into which the simulated pasture was divided (e.g. one 100 ha cell versus three 33.3 ha cells) also had strong influence (mean $|S| = 1.28$); as the number of cells increased, peak number of questing larvae decreased. Initial larvae per cow had a strong influence (mean $|S| = 1.14$); as cattle introduced more larvae, peak number of questing larvae increased. Habitat selection by the cattle herd had similar influence (mean $|S| = 1.06$); as cattle spent a greater proportion of the day in a grass rather than a mesquite habitat, peak number of questing larvae decreased. Other factors had a moderate influence on peak numbers of questing larvae (mean $|S| = 0.87$–0.44), such as the threshold CSDH at which larval death occurs, the proportion of *Bos indicus* in cattle genotypes, the larval attachment rate, and the incubation temperature at which the rate-controlling enzyme becomes half active and half low-temperature inactive (TL). Several factors had relatively little influence on peak numbers of questing larvae (mean $|S| = 0.28$–0.00), such as the time each day that cattle start a half-day stay each day in the mesquite half of a 50% grass/50% mesquite pasture, the mortality rate of engorged females, the proportion of pasture area in grass in a grass/mesquite pasture (in which the herd spent equal time in each habitat), the amount of time needed for newly hatched larvae to harden their exoskeletons and begin questing, and the threshold CSDH at which engorged female death occurs.

3.2. Comparison with laboratory data

The model was used to replicate experiments from the literature; predicted results were compared with those observed. A substantial body of laboratory data

allowed testing of the model's predictions of preoviposition duration, oviposition duration, daily egg production, conversion efficiency index, egg incubation duration, percentage egg hatch, hatch duration, larval longevity, engorged female detachment rates, and on-host mortality rates with datasets not used to develop the model.

3.2.1. Preoviposition duration

Data from Fujisaki et al. (1975), Davey et al. (1980a, 1980b), de la Vega et al. (1984), de la Vega and Díaz (1985), Davey (1988), and Barriga et al. (1995) were used to test model predictions of preoviposition duration at various combinations of temperature and RH (Fig. 2). The model tended to predict preoviposition duration relatively well, deviating from observations among these studies by a mean of +1% (1 S.D. = 17%) (Table 5). Predictions deviated most when simulating the colder bi-level temperatures of Davey (1988) (−30% at 30/15 °C, −20% at 25/10 °C, and +44% at 20/5 °C).

3.2.2. Oviposition duration

Data from Hitchcock (1955a), Davey et al. (1980a, 1980b), Ouhelli et al. (1982), Barriga et al. (1995), and Pereira (1998) were used to test model predictions of oviposition duration at various combinations of temperature and RH (Fig. 3). The model tended to underpredict oviposition duration, deviating from observations among these studies by a mean of −9% (1 S.D. = 20%) (Table 5). Predictions deviated most at 15 °C (+30%) and 27 °C (−33 to −42%) (circled, Fig. 3).

3.2.3. Daily egg production

Ouhelli et al. (1982) and Pereira (1998) examined daily egg production at 25 and 27 °C, respectively. When simulating the former experiment, the model predicted date of peak oviposition within 2

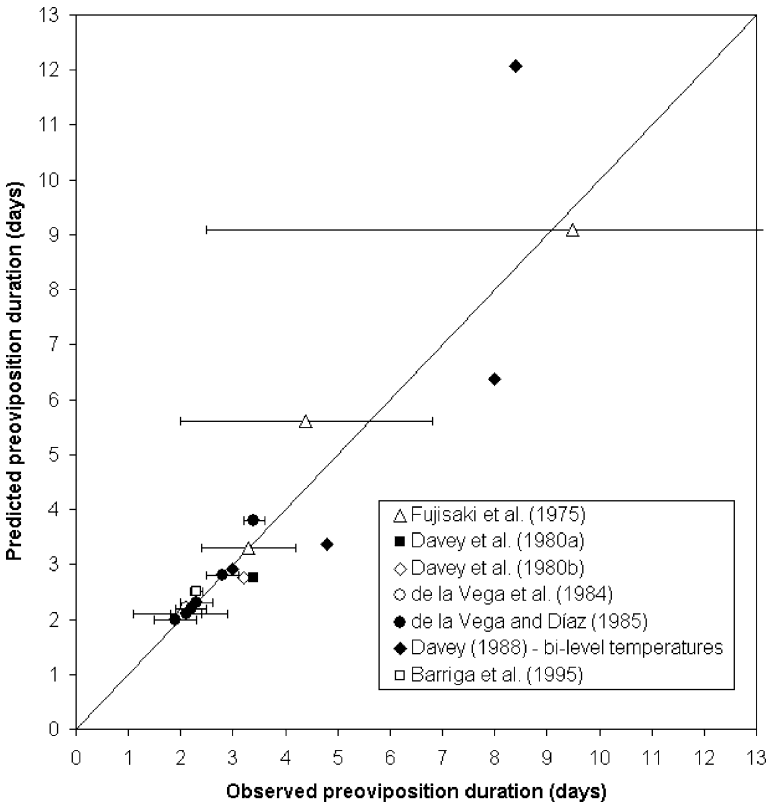

Fig. 2. Predicted preoviposition durations (days) plotted against observed means from seven laboratory experiments. Error bars show ±99.9% confidence intervals.

Table 5
Studies used to evaluate accuracy of stage-wise model output, the experimental designs simulated, and percentage over- or underprediction of observed mean values (mean and standard deviation if $n > 1$)

Model process tested	Study	Experimental design	Deviation from observed (mean ± 1 S.D. if $n > 1$)
Preoviposition duration	Fujisaki et al. (1975)[a]	Constant temperatures (15–30 °C) and RHs (53–100%)	+7 ± 14%
	Davey et al. (1980a)[b]	27 °C and 84% RH	−19%
	Davey et al. (1980b)[a]	27 °C and 80% RH	−14%
	de la Vega et al. (1984)[a]	30 °C and 100% RH	+5%
	de la Vega and Díaz (1985)[a]	Constant temperatures (24–36 °C) and RHs (88–100%)	+3 ± 5%
	Davey (1988)[b]	Bi-level temperature regimes and 92.5% RH[c]	−2 ± 33%
	Barriga et al. (1995)[a]	28 °C and 92% RH	+9%
Oviposition duration	Hitchcock (1955a)[a]	Constant temperatures (15.0–38.9 °C) and 95 or 99% RH	+1 ± 14%
	Davey et al. (1980a)[b]	27 °C and 84% RH	−40%
	Davey et al. (1980b)[a]	27 °C and 80% RH	−33%
	Ouhelli et al. (1982)[b]	25 °C and 84% RH	−4%
	Barriga et al. (1995)[a]	28 °C and 92% RH	−22%
	Pereira (1998)[a]	27 °C and 85–95% RH	−42%
Conversion efficiency index (CEI)	Bennett (1974)[a]	Temperatures cycling with 24 h period and amplitude of ±4.2 °C around means of 12.8–40.6 °C (ca. 85% RH)	+19 ± 62%[d]
	Davey et al. (1980a)[b]	27 °C and 84% RH	+6%
	Davey et al. (1980b)[a]	27 °C and 80% RH	−4%
	Ouhelli et al. (1982)[b]	25 °C and 84% RH	+30%
	Davey (1988)[b]	Bi-level temperature regimes and 92.5% RH[c]	−4 ± 4%
	Davey (1988)[b]	0–105 days at 12 °C, then 25 °C (all 92.5% RH)	+152 ± 118%[d]
	Barriga et al. (1995)[a]	28 °C and 92% RH	+34%
	Pereira (1998)[a]	27 °C and 85–95% RH	−7%
Incubation duration	Davey et al. (1980a)[b]	27 °C and 84% RH	−42%
	Davey et al. (1980b)[a]	27 °C and 80% RH	−29%
	de la Vega and Díaz (1985)[a]	Constant temperatures (24–36 °C) and RHs (88–100%)	−23 ± 12%
	Davey (1988)[b]	Constant temperatures (12–45 °C) and 92.5% RH	−21 ± 5%
	Davey (1988)[b]	Bi-level temperature regimes and 92.5% RH[c]	−15 ± 32%
	Davey (1988)[b]	0–105 days at 12 °C, then 25 °C (all 92.5% RH)	−4 ± 8%
	Barriga et al. (1995)[a]	28 °C and 92% RH	−39%
Percentage egg hatch	Hitchcock (1955a)[a]	Constant temperatures (16.7–36.7 °C) and RHs (70–99%)	+1124 ± 2143%[d]
	Davey (1988)[b]	Constant temperatures (12–45 °C) and 92.5% RH	−7 ± 5%[d]
	Davey (1988)[b]	Bi-level temperature regimes and 92.5% RH[c]	−36 ± 45%
	Davey and Cooksey (1989)[a]	0–105 days at 12 °C, then 25 °C (all 85% RH)	−63 ± 33%
	Strey et al. (1991)[b]	Constant temperatures (17–36 °C) and 85% RH	+1831 ± 3433%
	Barriga et al. (1995)[a]	28 °C and 92% RH	+88%
Larval longevity	Hitchcock (1955a)[a]	Constant temperatures (15–35 °C) and RHs (45–95%)	+452 ± 484%[d]
	Davey and Cooksey (1989)[a]	0–105 days at 12 °C, then 25 °C (all 85% RH)	−48 ± 47%
	Davey et al. (1991)[b]	Constant temperatures (30–35 °C) and RHs (32–97%)	+190 ± 430%[d]

[a] *B. microplus* data.
[b] *B. annulatus* data.
[c] 35/20 °C, 30/15 °C, 25/10 °C, 20/5 °C for 12/12 h.
[d] For non-zero observed values.

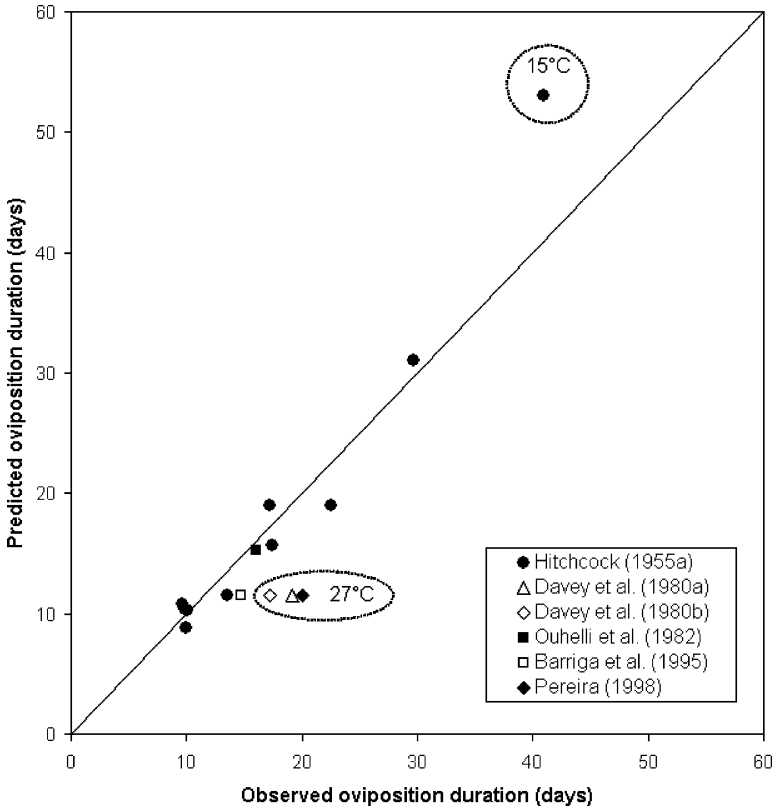

Fig. 3. Predicted oviposition durations (days) plotted against observed means from six laboratory experiments.

days (13% of oviposition duration) of the observed day and predicted the correct oviposition duration (Fig. 4a). In contrast, simulation of the latter experiment predicted peak oviposition within 1 day of the observed date but underestimated oviposition duration by 6 days (32%); however, only 4% of total mean observed eggs were laid in those final 6 days (Fig. 4b).

3.2.4. Conversion efficiency index

Data from Bennett (1974), Davey et al. (1980a, 1980b), Ouhelli et al. (1982), Davey (1988), Barriga et al. (1995), and Pereira (1998) were used to test model predictions of CEI at various combinations of temperature and RH (Fig. 5). Excluding the constant 12 °C experiment of Davey (1988), the model tended to overpredict CEI somewhat, deviating from observations among the other studies by a mean of +12% (1 S.D. = 46%) (Table 5). Predictions deviated most when simulating the experiment of Davey (1988) in which ovipositing females were held at 12 °C for 0–105 days before being placed at 25 °C (all 92.5% RH). As exposure to 12 °C increased (arrow, Fig. 5), overprediction of CEI increased.

3.2.5. Incubation duration

Data from Davey et al. (1980a, 1980b), de la Vega and Díaz (1985), Davey (1988), and Barriga et al. (1995) were used to test model predictions of incubation duration at various combinations of temperature and RH (Fig. 6). The model tended to underpredict incubation duration, deviating from observations among these studies by a mean of −17% (1 S.D. = 170%) (Table 5). Predictions deviated most at constant temperatures of 27–32 °C (−26 to −42%) and at the colder bi-level temperatures of Davey (1988) (−41% at 30/15 °C, −34% at 25/10 °C, and +30% at 20/5 °C).

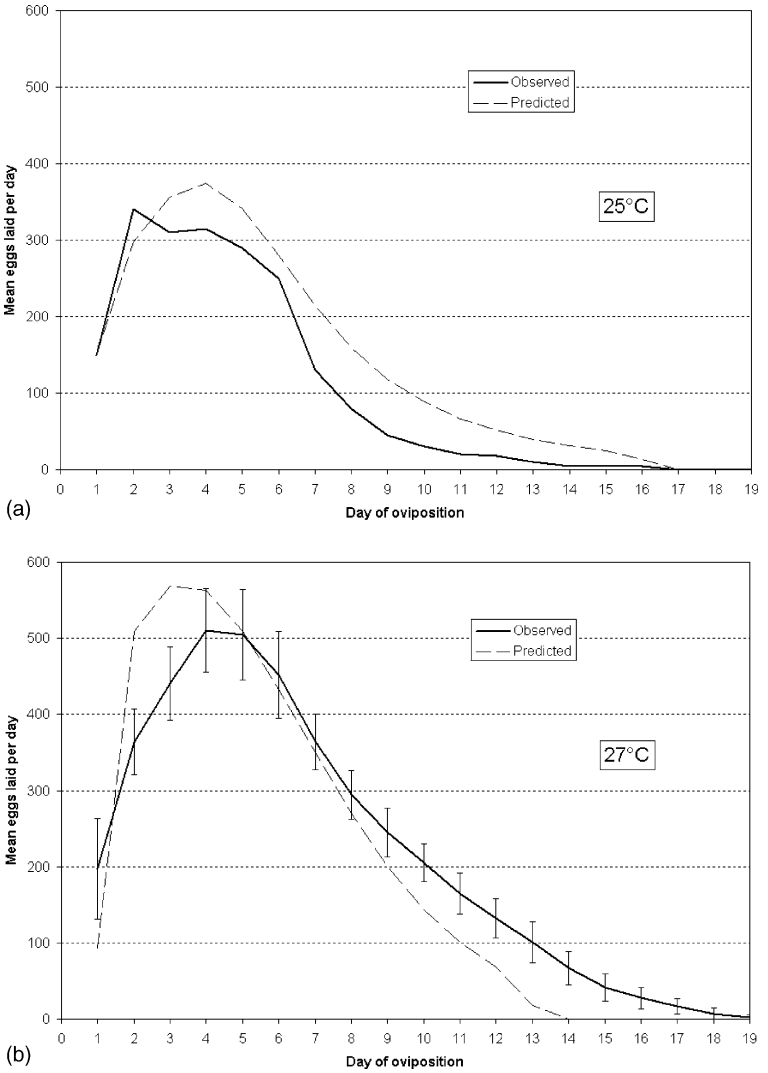

Fig. 4. Comparison of predicted numbers of eggs laid per day per female *B. microplus* at a constant temperature with those observed by (a) Ouhelli et al. (1982) and (b) Pereira (1998). Data from Pereira (1998) include ±99.9% confidence intervals.

3.2.6. Percentage egg hatch and hatch duration

Data from Hitchcock (1955a), Davey (1988), Davey and Cooksey (1989), Strey et al. (1991), and Barriga et al. (1995) were used to test model predictions of percentage egg hatch at various combinations of temperature and RH (Fig. 7). Excluding the experiments of Hitchcock (1955a) and Strey et al. (1991), the model tended to underpredict egg hatch percentage, deviating from observations among the other studies by a mean of −34% (1 S.D. = 49%) (Table 5). Predictions deviated most when simulating the experiments of Hitchcock (1955a) and Strey et al. (1991), which exposed eggs to constant temperatures and RHs. For simulations of Hitchcock (1955a), overpredictions of egg hatch percentage usually became vast (≫150%) when temperature ≤18.3 °C or RH ≤85%. For simulations of Strey et al. (1991), overpredictions of egg hatch percentage increased greatly as temperatures both increased and decreased from 33 °C. The model only partially captured effects of exposure to 15 °C in

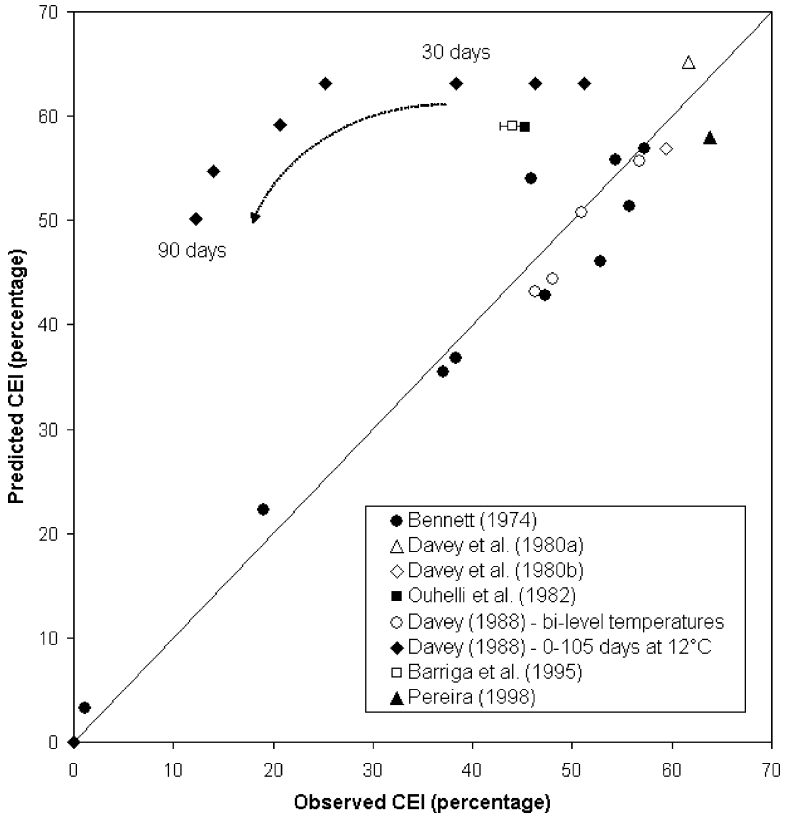

Fig. 5. Predicted conversion efficiency indices (percentages) plotted against observed means from eight laboratory experiments. Error bars show ±99.9% confidence intervals.

the constant-temperature experiment of Davey (1988), predicting 46% egg hatch where Davey (1988) observed none. In contrast, for the bi-level temperature experiment of Davey (1988), the model predicted no egg hatch at 20/5 °C where Davey (1988) observed 68%. Simulation of an experiment by de la Vega et al. (1984), who observed hatch rate of *B. microplus* eggs incubated at 30 °C, tested the equation driving the Weibull function for egg-hatch duration; the model overestimated hatch duration by 31%.

3.2.7. Larval longevity

Data from Hitchcock (1955a), Davey and Cooksey (1989), and Davey et al. (1991) were used to test model predictions of larval longevity at various combinations of temperature and RH. The model tended to overestimate larval longevity, sometimes greatly (Table 5). Hitchcock (1955a) examined survival of *B. microplus* larvae hatched at 35 °C and unknown RH under 27 combinations of constant temperature and RH. To simulate this experiment, we assumed that Hitchcock had incubated the eggs at 95% RH to maximize the number of eggs hatched; if so, the observed mean incubation duration of 17.2 days at 35 °C would have generated a CSDH during incubation of 843.7 mmHg h. Applying this value to the best-fit line, the model estimated a larval CSDH mortality threshold of 5275 mmHg h and a larval CDH mortality threshold of 17,081 °C h. Using these thresholds, the model usually overestimated larval longevity, especially at combinations of low temperatures (15 or 22 °C) and high RHs (circled, Fig. 8). The model reached the maximum allowed larval longevity (253 days) at combinations of 15 °C and RH ≥70% because both temperature and saturation deficit at these combinations fell below thresholds used to accumulate degree-hours and saturation-deficit

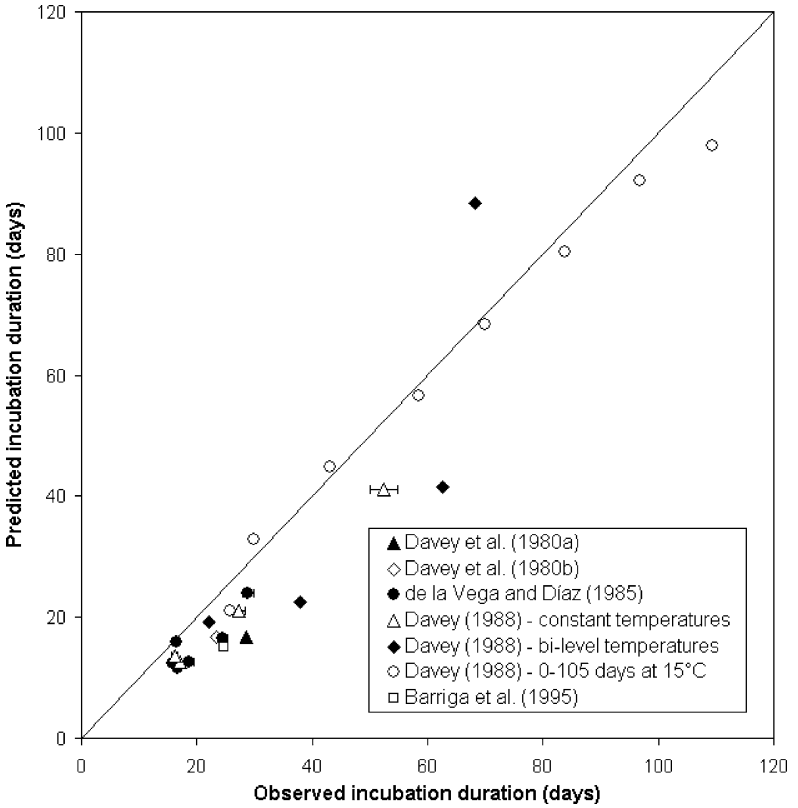

Fig. 6. Predicted egg-incubation durations (days) plotted against observed means from seven laboratory experiments. Error bars show ±99.9% confidence intervals.

hours. Model overestimates decreased, however, at the temperature and RH combinations at which the degree-hour submodel forced death of the larval cohort. Davey and Cooksey (1989) exposed *B. microplus* eggs, laid at 25 °C, to 12 °C for 0–105 days and then returned them to 25 °C to observe larval longevity. The model tended to underpredict mean larval longevity observed in this experiment, deviating from observed values by a mean of −48% (S.D. = 47%) (Table 5) (Fig. 8). The relatively high RH in this study (85%) meant that CDH alone determined larval longevity. In a third experiment, Davey et al. (1991) examined survival of *B. microplus*, *B. annulatus*, and *B. microplus* × *B. annulatus* hybrid larvae under 20 combinations of temperature (20–35 °C) and RH (32–97%). Unlike Hitchcock (1955a), however, Davey et al. (1991) observed larvae that had hatched from eggs incubated in each of the temperature–relative humidity combinations, rather than incubating all eggs at 35 °C. The incubation submodel was used to estimate the CSDH that *B. annulatus* larvae would have accumulated during incubation. The model tended to overpredict mean larval longevity (Table 5); however, the wide confidence intervals in the observed data often overlapped the predicted values (Fig. 8). The model tended to overestimate longevity most at 35 °C or RH ≤63%.

3.2.8. Female detachment rate and on-host mortality rate

Roberts (1968) observed detachment rate of engorged female *B. microplus* from *Bos taurus* cattle infested with 20,000 larvae. The model correctly predicted the observed day of peak detachment (on-host day 21) and predicted a cumulative detachment of 94% on the day that observed cumulative detachment reached 100% (on-host day 26). However, the model

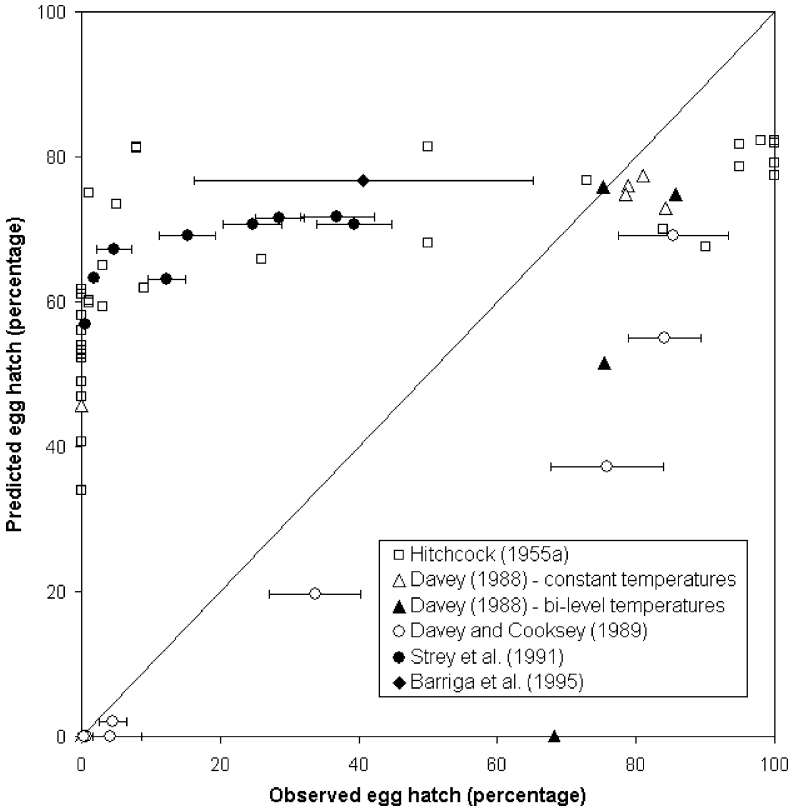

Fig. 7. Predicted egg-hatch percentages plotted against observed means from six laboratory experiments. Error bars show ±99.9% confidence intervals.

underestimated total number of females detaching by 63%, reflecting a total on-host mortality rate of 94%, higher than that (84%) displayed by the naïve *Bos taurus* cattle that Roberts (1968) used.

3.3. Comparison with field data

We next predicted durations of off-host preoviposition, incubation, and larval longevity in the field using data collected by Teel et al. (unpublished) at the Cattle Fever Tick Research Laboratory (USDA Agricultural Research Service), in Mission, Texas (26.2°N, 98.3°W). Teel et al. collected temperature and RH every 2 h at ground level in grass, mixed-brush, and mesquite habitats from 1987 to 1988. Field temperatures during the study varied greatly, often falling below 6 °C or exceeding 40 °C. On 13 dates during this period, they placed three vials, each containing 10 engorged *B. annulatus* females, on the soil of each habitat type and observed durations of preoviposition, incubation, and larval longevity. The model usually predicted preoviposition durations fairly well (Fig. 9a), deviating from observed mean values by a mean of +10% (S.D. = 46%) for spring and summer introductions (March–September) and −15% (S.D. = 22%) for autumn and winter introductions (October–February). The model tended to underestimate incubation durations (Fig. 9b), deviating from observed mean values by a mean of −28% (S.D. = 7%) for spring and summer introductions and −33% (S.D. = 20%) for autumn and winter introductions. The model tended to overestimate larval longevity (Fig. 9c), deviating from observed mean values by a mean of +75% (S.D. = 58%) for spring and summer introductions and +109% (S.D. = 81%) for autumn and winter introductions.

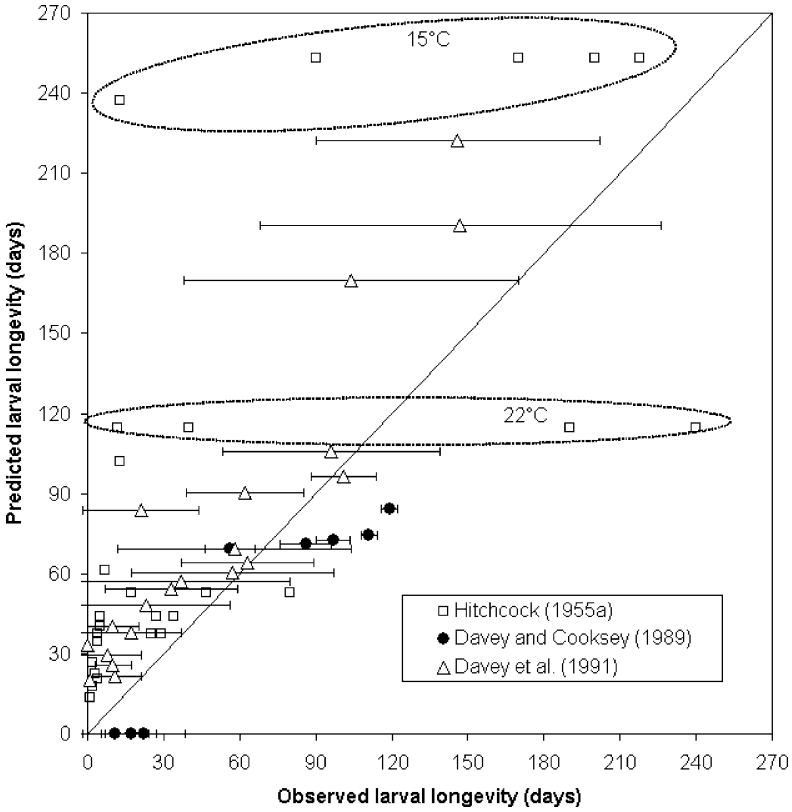

Fig. 8. Predicted larval longevities plotted against observed means from three laboratory experiments. Error bars show ±99.9% confidence intervals.

4. Model use

The model was used to predict the influence of habitat and cattle type on dynamics of *Boophilus* tick infestations on a hypothetical south Texas pasture. Model runs simulated 2-year periods beginning 1 January and used the temperature and RH field data of Fleetwood (1985). The simulated pasture contained a herd of 80 *Bos taurus* or *Bos indicus* cattle on a 100 ha pasture containing three habitat cells: 5 ha of grass (with water and bedding sites), 5 ha of mesquite (with shade), and 90 ha of either grass or mixed brush (with forage). Each cow began with 50 newly attached larvae. Cattle moved among habitat cells based upon seasonal daily activity-budgets predicted in a model of landscape use by south Texas cattle (Loza et al., 1992). Activity categories included times of grazing ("graze"), movement to a water source ("drink"), shade-seeking behavior ("shade"), and non-activity ("night" and "rest") (Fig. 10). During these latter three categories, the model reduced larval pick-up rate by 99% to represent minimal cattle movement, which reduces tick-host contact. Cattle in the model moved to the 5 ha grass cell for "night", "rest", and "drink" activities; the 5 ha mesquite cell for shade; and the 90 ha cell (grass or mixed brush) for grazing.

During the simulation with *Bos taurus* and the 90 ha grass cell, the tick population produced five generations each year, the maximum number observed in empirical studies (Evans, 1992). The 5 ha grass cell tended to have higher larval abundance, yet produced the lowest pick-up rates, because cattle moved little within the cell (i.e. "night", "rest", and "drink" activities) and larval densities often exceeded the threshold at which cattle could detect and avoid all larvae. The 5 ha mesquite habitat, though most favorable for tick

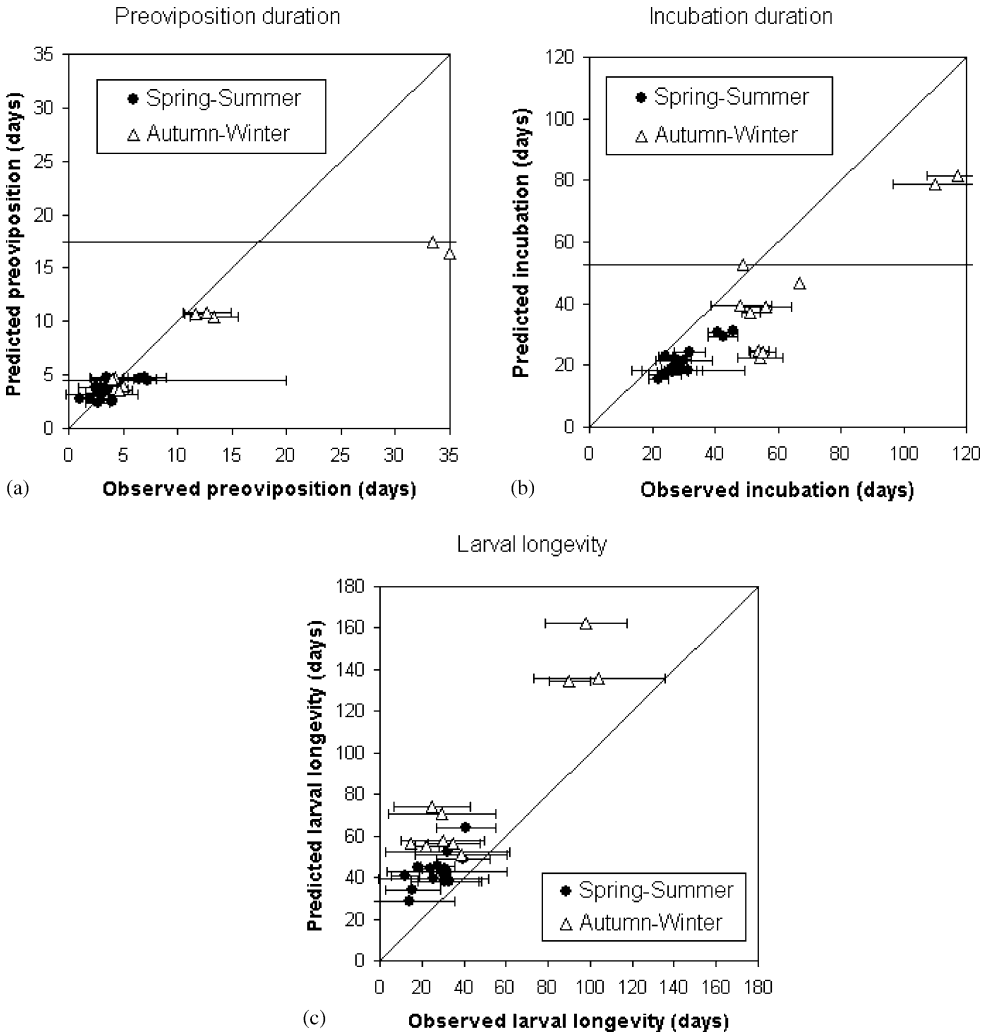

Fig. 9. Predicted (a) preoviposition durations, (b) egg-incubation durations, and (c) larval longevities plotted against those observed by Teel et al. (unpublished) in a field study of *B. annulatus*. Error bars show ±99.9% confidence intervals.

survival, usually contained the lowest larval population due to the relatively short time the herd spent there each day (<6 h) and the low pick-up rate induced by lack of movement when under shade. Number of larvae, however, did increase in mesquite in the summer, when cattle spent 6 h per day in the shade at times that coincided with hours of peak larval-questing activity. Larval density for the entire pasture peaked, during the second year, at 7 million questing larvae per ha. Host mortality caused by acute tick exposure (>3000 detectable ticks on host) occurred 12 times during the 2-year simulation, often repeating at 18-day intervals that corresponded to the time required for newly attached larvae to become detectable (Fig. 11a). Due to the high variability in number of detectable ticks, mortality due to chronic tick exposure never occurred in these simulations. Number of detectable ticks per cow peaked at 5438 and subsequently triggered host mortality (without host mortality, it would have peaked at an unlikely value of 23,370). Changing the 90 ha habitat from grass to mixed brush had relatively little influence in the *Bos taurus* scenario. Host mor-

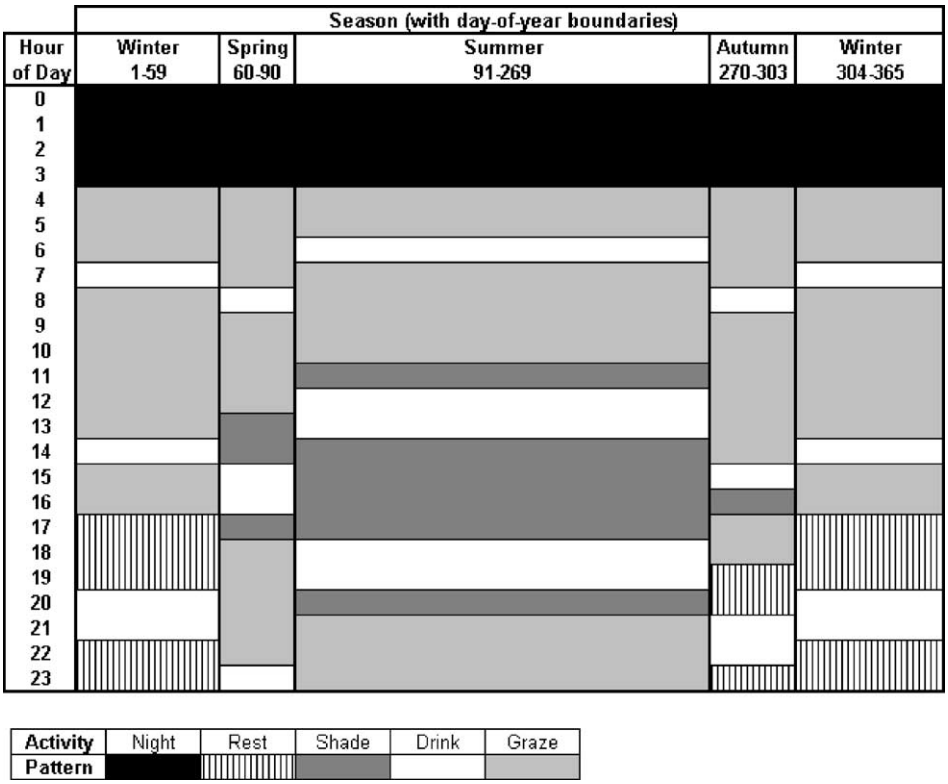

Fig. 10. Seasonal daily activity budget of the simulated cattle herd (from Loza et al., 1992).

tality increased in frequency, occurring 16 times during the 2-year simulation. Number of detectable ticks per cow peaked at 5900 before causing host mortality, 8% higher than it had peaked with the 90 ha grass pasture.

The simulation of *Bos indicus* and the 90 ha grass cell generated lower tick populations; for example, total larval density peaked at a level 37% smaller than that generated by *Bos taurus* hosts. Host mortality occurred less frequently: eight times during the 2-year simulation. Peak detectable ticks per cow also reached lower levels, peaking at 3632, 33% lower than the peak of detectable ticks on *Bos taurus* in the same habitat configuration (Fig. 11b). Finally, simulating *Bos indicus* in the 90 ha mixed-brush cell yielded patterns consistent with previous simulations. Total number of questing larvae increased when compared to *Bos indicus* that grazed in the 90 ha grass habitat, but decreased when compared to any of the *Bos taurus* simulations. Number of detectable ticks per cow followed the same pattern, peaking at 4516. None of the tick populations died out during any of these 2-year simulations.

5. Discussion

5.1. Sensitivity analysis

Sensitivity analyses revealed the great importance of temperature and RH on tick population dynamics. In a simulated mesquite pasture, temperature and RH ranked as the first and third most influential factors, respectively. When simulating a grass pasture (data not shown), which had higher temperatures and lower RHs, peak numbers of questing larvae became more sensitive to RH (ranked first) than to temperature (ranked second), a reversal of ranks that highlights the

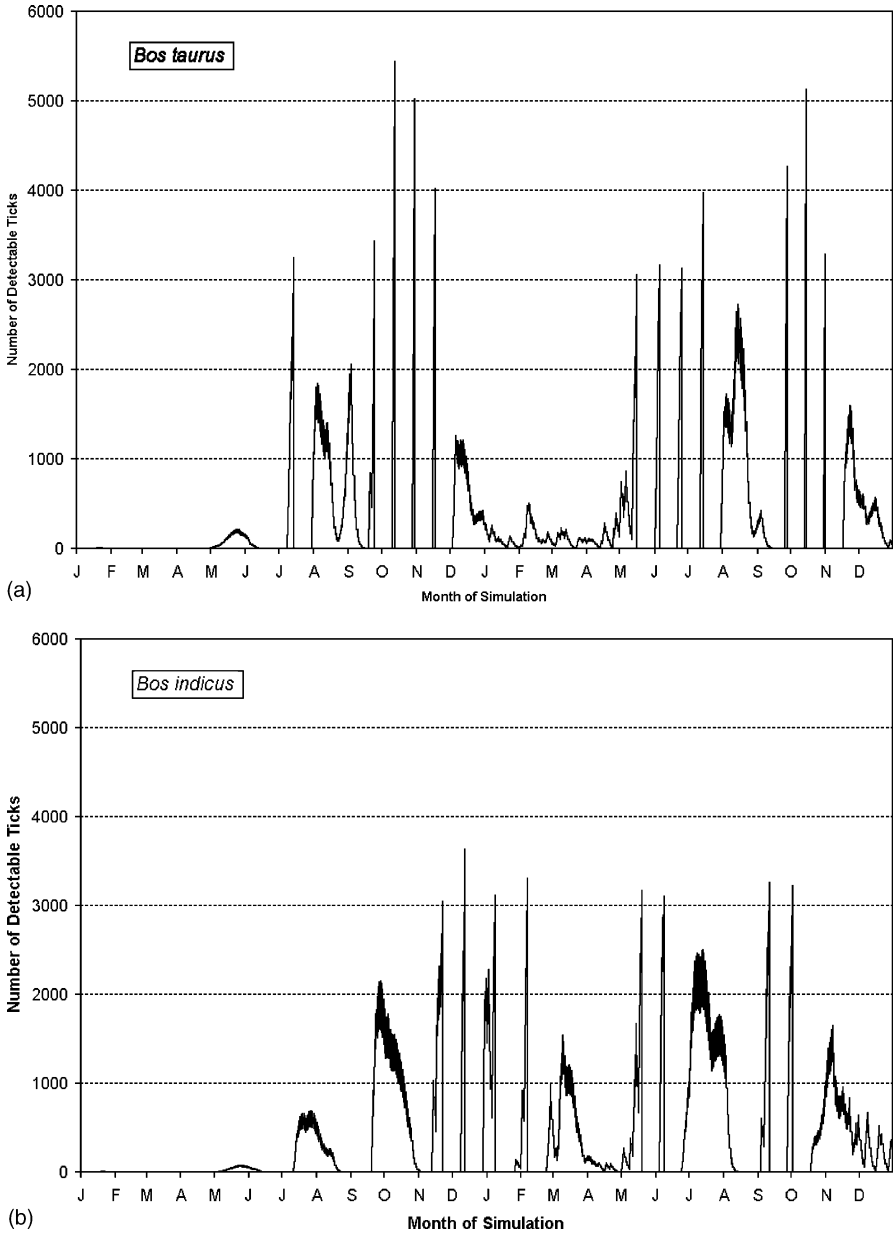

Fig. 11. Time series of detectable ticks per cow during a 2-year simulation of *Boophilus* infesting 80 (a) *Bos taurus* or (b) *Bos indicus* cattle in a 100 ha pasture with 95 ha of grass and 5 ha of mesquite.

importance of tick water-balance at higher temperatures. Given observed differences in temperature and RH by habitat type, use of ground-level *microclimate* data instead of regional *macroclimate* or local *mesoclimate* data seems to capture the influence of vegetation cover and provide better estimates of weather experienced by ticks (Daniel, 1978). Though microclimate temperature and RH in south Texas show moderate to strong correlations with macroclimate temperature and RH ($r = 0.843$ and 0.671, respectively) (Fleetwood,

1985), models using macroclimate data may estimate off-host development and mortality rates incorrectly, particularly where several habitat types exist on the landscape. In the field, plant phenology may play a role in the influence of vegetation; for example, mesquite habitats may experience greater fluctuations in temperature and RH than mixed-brush communities because mesquite plants can shed their leaves when temperatures become too hot (Fleetwood, 1985). In addition, buffelgrass, a common forage species in south Texas, quickly can produce abundant shoot growth in response to rainfall events (Martin-R et al., 1995).

The importance of the number of cells used to represent the pasture emphasizes the influence of the spatial component of this model. Dividing the tick population into subpopulations decreases their host-encounter rates and increases the importance of herd movement among habitat cells, as indicated by the sensitivity of peak numbers of larvae to cattle habitat selection (i.e. proportion of day spent in a grass versus mesquite habitat). The strong influence of initial number of larvae reveals the system's sensitivity to initial conditions of an infestation. The high to moderate sensitivity of peak number of larvae to engorged female mass (which influences fecundity), the threshold CSDH at which larval death occurs, and the proportion of *Bos indicus* in cattle genotypes (which influences on-host survival rates) agrees with the elasticity analysis of the BCTSIM model (Mount et al., 1991) done by Dixon et al. (1997). They found that the *B. microplus* population growth rate in BCTSIM appeared most sensitive to the survival and development of on-host ticks, female fecundity, and off-host survival of larvae (Dixon et al., 1997). Decreasing the egg-development temperature TL to −1.8 °C had little effect on number of questing larvae, but increasing it to 24.9 °C decreased number of questing larvae because it raised half-activation temperature high enough to slow incubation greatly at most ambient temperatures.

5.2. Comparison to laboratory data

Comparison of model predictions to observed laboratory and field data revealed some important strengths and weaknesses of the model. The model tended to predict preoviposition duration relatively well but deviated most from observed mean values when simulating exposure to fluctuating temperatures down to 5–15 °C. Built with constant-temperature data above 12 °C, the preoviposition submodel may not capture completely the effects of exposure to and recovery from cold temperatures. The model tended to underpredict oviposition duration, especially at the benign (for *Boophilus* ticks) temperature of 27 °C. The curves used to fit oviposition rates at 25 and 27 °C in the oviposition submodel have higher *y*-intercepts than those used for other temperatures (Table 2), which may have led to the model's underpredictions at those temperatures. The model tended to predict daily egg production acceptably for the first several days of oviposition, but its general underprediction of oviposition duration led it to underpredict number of eggs produced toward the end of oviposition. The model tended to overpredict CEI to some extent. Although the CEI submodel captured cold exposure well when simulating the fluctuating-temperature experiment of Bennett (1974), it failed to capture effects of cold in the constant 12 °C experiment of Davey (1988). This model limitation may have little effect when simulating south Texas pastures (microclimate data from Fleetwood (1985) show no period of temperatures ≤12 °C lasting longer than 55 h), but may become important if simulating areas in which temperature begins to limit the geographical distribution of *B. microplus* or *B. annulatus*. The model tended to underestimate egg incubation durations, especially at fluctuating colder temperatures, but appeared more accurate than other submodels in predicting constant cold-temperature influences. The model's difficulty in predicting incubation at constant temperatures of 27–32 °C may have resulted from developmental differences in the *B. annulatus* strain that Strey et al. (1991) used to develop the incubation submodel and the strains of *B. microplus* or *B. annulatus* used in the experiments simulated. Underestimates of incubation duration at colder temperatures may have occurred, in part, because Strey et al. (1991) had to estimate, rather than observe, day of first hatch at 12 and 14 °C, which could have compromised the predictive ability of their incubation model at colder temperatures. Yet, cold-induced mortality may skew estimates of incubation period at low temperatures, effectively selecting for those individuals that can develop at colder temperatures (Davey, 1988). Further, the incubation submodel may underpredict in-

cubation duration because the eggs Strey et al. (1991) used to develop their model had a relatively uniform age (laid on days 3 and 4 of oviposition) and "optimal survival potential". Finally, the incubation model does not reflect any egg development that occurred during 1–2 days of oviposition at 27 °C (Strey et al., 1991).

Model predictions deviated most from observations when predicting percentage egg hatch, especially at temperatures ≤20 °C or high saturation deficits in the constant temperature and RH experiments of Hitchcock (1955a) and Strey et al. (1991). Strey et al. (1991) spread egg masses into thin layers for ease of measuring egg hatch progression; this manipulation may have increased moisture loss, and therefore mortality rate, of egg masses. The poor fit of the curve used to predict egg-cohort mortality ($R^2 = 0.402$) failed to capture most of the variability observed between egg CSDH and egg mortality, suggesting that other factors have a strong influence; additional analysis of the data (Teel et al., unpublished) may reveal these factors. Unlike the constant temperature and RH experiments of Hitchcock (1955a) and Strey et al. (1991), the experiment of Teel et al. (unpublished) used to develop the model relationship between egg CSDH and egg mortality included variable temperatures and RHs. Fluctuating temperature and RH may allow recovery from unfavorable microclimate conditions, recovery that may not occur under constant temperature and RH. Overestimates of larval longevity seemed greatest at temperatures <20 °C and RHs >70%, which generated abnormally low mortality rates in the submodels that calculated CSDH and CDH. As with egg mortality, the poor fit of the curves used to predict larval longevity ($R^2 = 0.339$ and 0.195) failed to capture most of the observed variability in larval longevities; re-analysis of the data (Teel et al., unpublished) seems warranted. Further, underestimates of incubation time contributed to overestimates of larval longevity by overestimating the CSDH and CDH required for larval cohort mortality. As discussed later, constant temperatures and RHs that lay close to biological thresholds led the model to overestimate larval longevity because the model did not represent another cause of larval mortality: energy exhaustion. Finally, the model tended to underestimate the number of engorged females detaching from a host, but it may have relatively little effect given the low sensitivity of peak numbers of questing larvae to engorged female mortality rate.

5.3. Comparison to field data

Compared to simulations of laboratory experiments, the model generally predicted field-observed preoviposition similarly well, underpredicted incubation duration somewhat more, and overpredicted larval longevity somewhat less. Predictions for these stages tended to worsen when simulating tick introductions during the colder autumn and winter period (October–February), which had a mean temperature of 16.9 °C (S.D. = 7.8 °C) among all habitat types. Increasing the incubation temperature at which the rate-controlling enzyme is half active and half low-temperature inactive (TL) to 22.8 °C greatly improved predictions of incubation duration (data not shown), but such a value seemed neither justifiable nor biologically reasonable for *Boophilus* ticks.

5.4. Model use

The simulated tick population during the first year after introduction consisted of five generations that steadily increased in size. During the second year, however, population size showed no consistent pattern. Predicted population dynamics appeared to show transitional and quasi-stable states: after 3–4 years of simulated dynamics (data not shown), numbers of ticks in each life stage reached approximately the same sizes each year. The temporal progression and abundances of tick stages appeared reasonable. Imposition of host mortality limited detectable-tick burdens on *Bos taurus* to 5438, about twice the maximum number observed in the field. Simulations with *Bos indicus* hosts predicted lower peak tick burdens (maximum of 4516), but this represents overestimation by at least one order of magnitude. Differences between tick population dynamics when infesting either *Bos taurus* or *Bos indicus* cattle lay primarily in the on-host mortality rates (Table 3). Fewer larvae survived to adulthood on *Bos indicus* hosts, providing negative feedback that subsequently decreased the number of off-host ticks in the field. As brush content of the pasture increased, host mortality occurred more often due to the larger tick populations caused by lower temperatures and higher RHs at ground level.

5.5. General considerations

Datasets used to develop or evaluate the model often were reported at intervals coarser than desired. The vast majority of studies reported daily rates or durations, which may have introduced prediction errors when converted to hourly rates or compared to hourly durations. Further, certain measurements obscured the effects or durations of different processes. For example, observations of CEI at extreme temperatures usually did not discriminate between (1) reduction in mass of eggs produced due to early female mortality, and (2) reduction due to decreased egg production per female. Similarly, observed larval longevities are influenced not only by larval mortality rates, but by durations of oviposition, time to first-hatch, and complete egg hatch. In egg masses with long incubation times, the first larvae may emerge and die before later larvae emerge, especially under conditions of high saturation deficit, thus confounding effects of incubation rate and larval mortality rate. Observing mortality rates of larvae divided into daily cohorts by hatch day would help separate effects of these rates, providing better data for this model.

Conceptually, the number of habitat cells represented in a pasture had a large effect on population dynamics. More cells, regardless of type, reduced estimates of tick population size. Using a greater number of cells seems the better strategy, for it reflects reality better, in which larvae exist as "hotspots" in a pasture and depend entirely upon the pattern of host movement to encounter a host. Simulating a pasture divided into only three cells overemphasized the availability of hosts to larvae because the herd picked up a proportion of all questing larvae in each cell it visited, thereby reducing the importance of host habitat use. In the real system, as in the model, habitat sizes seem to have less importance than the proportion of time hosts spend in each of them (Stuth, 1991). Because hosts serve as the sole connection between tick generations, host behavior has a strong influence in this system, determining which habitats detaching ticks enter and the probability that larvae find a host. Unfortunately, time and software limitations prevented creation of more than three cells in this model. Increasing the number of cells in the pasture may require adjusting the equations governing host-finding rate but should reduce the model's overprediction of on-host tick burdens. Some field studies of *Boophilus* spp. (e.g. Davey et al., 1994) have focused on the importance of different habitat types on tick survival and development but have placed little emphasis on habitats with woody vegetation. Brush encroachment has occurred on most south Texas pastures since eradication of *Boophilus* (Archer et al., 1988), increasing their potential to sustain high tick populations should *Boophilus* ticks reinfest them (Teel et al., 1994). Given the 2-year period simulated, we felt comfortable keeping habitat type constant; however, simulations over longer time periods may require incorporation of a more dynamic, spatially explicit vegetation model (Holt et al., 1995), such as that developed by Grant et al. (1999).

The model had difficulty capturing the influence of extreme temperatures, especially constant ones, on egg development, egg mortality, and larval mortality rates. Laboratory studies at constant extreme temperatures and RHs, however, may bias mortality estimates because most do not allow for recovery from extreme conditions, as can occur under fluctuating field conditions (Utech et al., 1983; Nedved et al., 1998). Nonetheless, obtaining additional data at extreme temperatures could improve model predictions, especially for regions near the edge of the geographic distributions of *B. annulatus* or *B. microplus*. Finally, representing larval energy reserves and energy use rates seems a necessary model addition because CSDH and CDH do not predict larval mortality well, especially at low temperatures and high RHs. Using maximum lipid content and lipid-use rates to provide upper limits on larval longevity seems better than specifying a maximum chronological longevity by month of egg hatch and has been used to estimate maximum longevity of *Ixodes ricinus* nymphs (Steele and Randolph, 1985).

5.6. Future directions

Model predictions could be improved with data that scarcely exist, if at all, for *B. microplus* or *B. annulatus*; hence, designing experiments to collect these data could serve as future research priorities. In order of decreasing importance, incorporation of the following empirical data could help improve the model's accuracy:

- The initial lipid content of a *Boophilus* larva, the influence of temperature and RH on the rate at which

it uses lipid reserves, and the lipid content at which a larva dies of energy exhaustion.
- The relationships between both cumulative saturation-deficit hours and cumulative degree-hours and mortality rates of daily cohorts off-host females, eggs, and larvae, especially at extreme temperatures ($\leq 14\,^{\circ}C$ or $\geq 40\,^{\circ}C$) and RHs (<70%).
- The rates at which off-host females, eggs, and larvae can recover from extreme temperature and RH exposures (e.g. as done for the collembolan *Orchesella cincta* (Nedved et al., 1998)).
- The influence of cumulative saturation-deficit hours and cumulative degree-hours experienced as an egg on subsequent longevity of a larva.

To improve the realism and accuracy of this model, we plan the following improvements:

(1) Explicitly represent more habitat cells. Sensitivity analyses highlighted the strong influence of cell size and host movement on pick-up rate. Conceptually, representing the habitat with smaller areas increases the importance of explicit cattle movement, because larval pick-up no longer depends on average movement within a cell; instead, it depends upon specific movement among cells.
(2) Increase complexity of the cattle submodel. Replacing the driving variable that determines cattle-herd location with a submodel that would calculate herd location as a function of physiological requirements and forage availability (e.g. Folse et al., 1989) would improve the model's ability to simulate influence of weather on cattle movement. Explicitly representing tick pick-up and detachment from each cow in the herd as a function of position in herd hierarchy also would increase the model's realism and possibly improve its predictions.
(3) Add the influence of energy use when predicting engorged female, egg, and larval mortality. Limiting larval longevity as a function of estimated lipid reserves and lipid-use rates may prove helpful.
(4) Add stochasticity to the model. Organisms in this system exhibit relatively large amounts of natural variation, especially in mortality and development rates. We captured none of this with our deterministic models, but doing so could provide better bounds on estimates and could describe some of the uncertainty in the system. In particular, deterministic models of *Boophilus* ticks in marginal areas can use stochastic elements to provide probabilities of persistence and estimates of population size (Sutherst, 1983).
(5) Simulate dispersal of *Boophilus* by wildlife. White-tailed deer (*Odocoileus virginianus*), more abundant in south Texas now than before the eradication program began, can disperse *Boophilus* ticks (Gray et al., 1979), which could compound the difficulty of eradication efforts.
(6) Include representation of acaricide or vaccine treatments. These activities often represent the most important management tools for eradicating or controlling *Boophilus* tick populations, respectively, and exist in several *Boophilus* tick models (e.g. Floyd et al., 1995; Lodos et al., 2000; Corson et al., 2001).

With these improvements, this physiologically based, spatially explicit model may become a better instrument for evaluating the effects of *Boophilus* tick eradication or control programs.

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